STUDIES ON THE CALIFORNIAN SPECIES OF STIPA (GRAMINEAE)[1]

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I. The Ratio of Lemma to Palea Length as a Taxonomic Character

The genus *Stipa,* according to Hitchcock (1950), has in California nineteen species and four varieties—about one-half of the number of species reported for the entire United States. In addition to the taxonomic treatment given by Hitchcock, the Californian species have been studied cytologically by Stebbins and Love (1944), who have made most of the available chromosome counts of the species. There does not appear to be, incidentally, any evident correlation between chromosome number and the grouping of species indicated by other criteria.

In the course of morphological and anatomical investigations made by the author while studying the Californian species of *Stipa,* it was found that the ratio of the length of the lemma to that of the palea (hereafter expressed as L:P) was of significance. On the basis of this ratio, the Californian species may be divided into the following three groups:

Group 1	Group 2	Group 3
L:P less than 2.0	L:P 2.0–4.0	L:P more than 4.0
S. comata	*S. arida*	*S. cernua*
S. comata intermedia	*S. californica*	*S. lepida*
S. coronata	*S. columbiana*	*S. lepida Andersonii*
S. latiglumis	*S. columbiana Nelsoni*	*S. pulchra*
S. Lemmoni	*S. coronata*	
S. Lettermani	*S. coronata depauperata*	
S. pinetorum	*S. diegoensis*	
S. speciosa	*S. Elmeri*	
S. Stillmanii	*S. latiglumis*	
S. Thurberiana	*S. occidentalis*	
	S. pulchra	
	S. speciosa	
	S. Williamsii	

Table 1 shows the L:P ratio for each of the species and varieties listed above, as well as the most frequent value in each case. As indicated in figure 1, the division of the species and varieties into the three groups is not perfect because of the existence of a few cases of overlapping in values. Thus, *S. coronata, S. latiglumis,* and *S. speciosa* must be included both in groups 1 and 2.

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Table 1. Ratio of Lemma over Palea in the Californian Species of Stipa.

Species	Number of specimens studied	L:P	Most frequent values
S. arida Jones	17	2.0–2.7	2.4
S. californica Merr. & Dav.	44	2.0–3.2	2.4–2.5
S. cernua Steb. & Love	20	4.0–8.0	6.0–6.5
S. columbiana Macoun	33	2.2–3.2	2.5
S. columbiana var. *Nelsoni* Hitch.	4	2.2–3.0	2.8
S. comata Tr. & Rupr.	28	1.3–1.6	1.5
S. comata var. *intermedia* Scrib.	9	1.4–1.6	1.5
S. coronata Thurb.	46	1.6–2.2	1.8
S. coronata var. *depauperata* Hitch.	22	1.6–2.5	2.3
S. diegoensis Swallen	8	2.0–2.2	2.0
S. Elmeri Piper & Brodie	28	2.0–3.5	3.0
S. latiglumis Swallen	9	1.7–2.0	1.8
S. Lemmoni (Vasey) Scrib.	44	1.2–1.6	1.4
S. lepida Hitch.	21	4.1–6.0	5.0
S. lepida var. *Andersoni* Vasey	12	4.0–5.5	4.2
S. Lettermani Vasey	32	1.2–1.7	1.4–1.6
S. occidentalis Thurb.	57	2.0–3.5	2.3
S. pinetorum Jones	21	1.1–1.7	1.4
S. pulchra Hitch.	60	4.0–5.7	4.5
S. speciosa Tr. & Rupr.	57	1.5–3.3	2.5
S. Stillmanii Boland.	6	1.0–1.1	1.1
S. Thurberiana Piper	33	1.1–1.7	1.5
S. Williamsii Scrib.	6	2.5–3.0	3.0

Much more reliable, however, is the arrangement of the species into two groups, the former comprising those in which the L:P ratio is less than 4.0, and the latter consisting of those in which the L:P ratio is 4.0, or more than 4.0. Furthermore, this division corresponds perfectly with a division of the species into two classes based upon the type of inflorescence. As indicated by the following key, the combination of these two characters, supplemented by other characters which have been more commonly used to delineate species, makes possible a new arrangement of the Californian species of *Stipa*.

A. Panicle narrow, contracted or slender, sometimes more expanded; L:P ratio less than 4.0.
  B. Lemma densely appressed-villous, with white hairs 3–4 mm. long rising above the summit in a pappus-like crown.
    C. Lemma ca. 8 mm. long; awn 4–5 cm. long ..... *S. coronata*
    CC. Lemma up to 6 mm. long; awn ca. 2 cm. long ..... *S. pinetorum*
  BB. Lemma sparsely appressed-pubescent to glabrate, never villous with long hairs.
    D. Awns pubescent, most commonly plumose.
      E. First segment of the once-geniculate awn strongly plumose, the ascending hairs 5–8 mm. long ..... *S. speciosa*
      EE. First segment of the awn conspicuously pubescent, generally plumose but the hairs 2 mm. long or less.
        F. Lemma bilobed at summit, the lobes extending into two lateral awns 2–3 mm. long on each side of the central awn ..... *S. Stillmanii*
        FF. Lemma entire or only obscurely lobed at summit.
          G. Ligule hyaline, 3–6 mm. long ..... *S. Thurberiana*

GG. Ligule opaque, minute, less than 3 mm. long.
H. Palea 4–5 mm. long ..... *S. latiglumis*
HH. Palea up to 3 mm. long.
I. Sheaths glabrous.
J. Hairs on upper part of lemma longer than those below; hairs of awn rather short ..... *S. californica*
JJ. Hairs of lemma uniformly short; hairs of awn rather long..... *S. occidentalis*
II. Sheaths pubescent ..... *S. Elmeri*
DD. Awns scabrous to nearly glabrous, rarely appressed-hispid, not plumose.
K. Mature lemma pale or becoming brownish, mostly more than 1 cm. long..... *S. comata*
KK. Mature lemma yellowish, not more than 8 mm. long.
L. Lemma broad; first glume 5-nerved..... *S. Lemmoni*
LL. Lemma narrow; first glume 3-nerved.
M. Palea much smaller than lemma, L:P 2.0–4.0; lemma short-hirsute throughout.
N. Culms densely pubescent below the nodes; palea 3–4 mm. long..... *S. diegoensis*
NN. Culms glabrous below the nodes; palea 2.5 mm. long or less.
O. Awn 4–6 cm. long, obscurely geniculate, the terminal segment flexuous; lemma short-hirsute except near the glabrous apex..... *S. arida*
OO. Awn usually less than 5 cm. long; if 4 cm. long, twice-geniculate, the terminal segment essentially straight.
P. Sheaths, at least the lowermost, pubescent ..... *S. Williamsii*
PP. Sheaths glabrous ..... *S. columbiana*
MM. Palea nearly equaling lemma, L:P less than 2.0; hairs at summit of lemma longer than those of the body ..... *S. Lettermani*
AA. Panicle broad, open, loose, the branches spreading, L:P 4.0 or more than 4.0.
Q. Lemma less than 7 mm. long; awn up to 4 cm. long ..... *S. lepida*
QQ. Lemma more than 7 mm. long; awn much more than 4 cm. long.
R. Lemma slender, cylindrical; middle culm leaves 1.2–2.4 mm. broad; foliage usually glaucous; awn slender, flexuous beyond the second bend, mostly 9–12 times the length of the lemma ..... *S. cernua*
RR. Lemma fusiform; middle culm leaves 2.4–6 mm. broad; foliage usually green; awn stout and stiff, mostly 7–9 times as long as the lemma..... *S. pulchra*

II. The Occurrence of Stipa Lettermani Vasey in California

Stipa Lettermani Vasey, a perennial grass 20–30 cm. tall producing culms in large tufts, has often been reported for California where it is stated to grow on open ground or in open woods at high altitudes. Its occurrence in the state is indicated by Hitchcock (1950), and the numerous Californian collections identified as this species by various authorities suggest that it is widespread in the state. *Stipa californica* Merr. & Davy, another perennial grass which has been differentiated from *S. Lettermani* primarily on the basis of differences in the pubescence of the awns, has been generally accepted to be widespread at lower altitudes than *S. Lettermani.*

On the basis of the L:P ratio already discussed as well as other morphological and anatomical data gathered by the author during the course of his study of the Californian species of *Stipa,* it has been possible to clarify

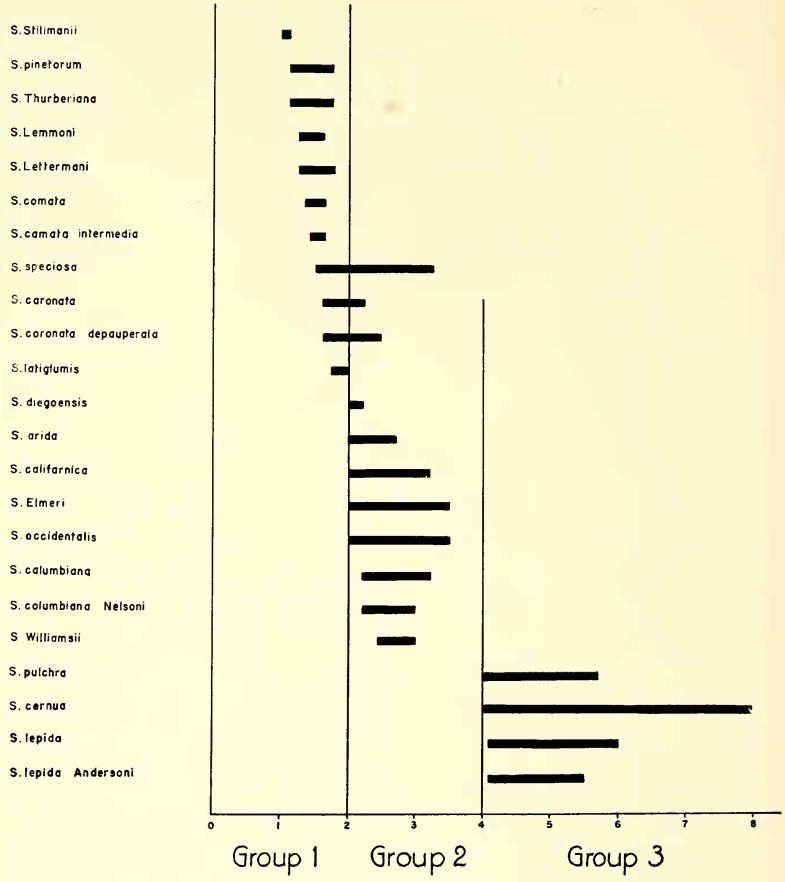


FIG. 1. The ratio of lemma to palea length in the Californian species of *Stipa*.

our concept of these two species. Although a comparison of the morphological characters of *S. Lettermani* and *S. californica* suggests a general similarity on such characters as panicle type, texture of the glumes, pubescence of the lemma, and the length of the callus, a number of diagnostic characters (table 2) are present. Of these, the highly specific and extremely different L:P ratio is outstanding.

In habit, *S. Lettermani* appears to be relatively similar throughout its range being of medium height. *Stipa californica* is much more variable; in altitudes from 4,000 to 6,000 feet it grows in open pine woods and is a robust plant with long leaves and culms 80–100 cm. high, and at higher altitudes there is a gradual transition to dwarfed and subalpine types growing in open places. These have much shorter leaves and culms which may not exceed 30–40 cm. It is this dwarf type which is confused with *S. Lettermani*.

Stipa Lettermani, S. californica, and *S. Elmeri* (the last differing sharply in other characters and hence not confusable with the other two) are the only species of the genus in western North America characterized by possessing two kinds of hairs on the lemma, a feature which has been employed to distinguish the two former species from such close relatives as *S. occidentalis* and *S. columbiana.* Thus, in *S. Lettermani* and in *S. californica,* the body of the lemma (including the callus) is covered with sparse, stiff, white hairs, which increase in length toward the apex and culminate in a conspicuous terminal brush of longer hairs. The two species differ in lemma pubescence, however, for in *S. californica* either the hairs on the body of the lemma or the apical ones are longer and thicker than those of *S. Lettermani* (table 2).

Table 2. Comparison of Principal Diagnostic Characteristics of Stipa Lettermani and Stipa californica.

Structure	*Stipa Lettermani*	*Stipa californica*
Leaves	Green, slender, involute, 20–30 cm. long, 2.0–2.2 mm. broad, throughout culms	Green or somewhat glaucous, blades flat, with tendency to become involute, 10–15 cm. long, 1.5–4.0 mm. broad
Size of glumes	Glumes equal, 7.0–9.0 mm. long	Glumes slightly unequal, upper 8–13 mm. long, lower 7.5–12.0 mm. long, sometimes equal
Length of lemma	4.5–6.0 mm.	5.0–7.5 mm.
Width of lemma (unrolled)	1.6–2.0 mm.	1.9–2.2 mm.
Hairs at apex of lemma	1.3–1.7 mm. long, 10–19μ thick	1.5–2.2 mm. long, 20–30μ thick
Hairs on body of lemma	0.8–1.3 mm. long, 8–16μ thick	0.4–0.6 mm. long, 10–18μ thick
Lobes of lemma	0.8–1.0 mm. long	0.5–0.7 mm. long
Length of palea	3.5–4.5 mm.	2.0–3.0 mm.
L:P ratio	1.2–1.7	2.0–3.2
Pubescence of awn	Scabrous below first bend, glabrous on other two segments	First and second segments conspicuously or weakly pubescent, third segment scabrous

The pubescence of the awns may be considered the most reliable of the traditional criteria for distinguishing the two species. In *S. Lettermani* the first two segments of the awns are glabrous, and the third segment scabrous; in *S. californica* the first two segments are described as conspicuously plumose, the third scabrous. The chief confusion has occurred in the reference to *S. Lettermani* of plants which show a manifest pubescence on the first two segments, but in which the awn is not conspicuously plumose. In all instances, these plants actually belong to *S. californica,* the two first awn-segments of *S. Lettermani* being truly glabrous or essentially so.

A more reliable and easily employed criterion for separating the two species is provided by the absolute and comparative length of the palea. Measurements of some thirty-five collections of *S. californica* from throughout its range have shown the palea to vary in length from 2.0–3.0 (—3.2) mm., that is, the palea is rather short in comparison with the lemma. In *S. Lettermani,* on the other hand, the usual length of the palea is (3.0–) 3.5–4.5 (–5.0) mm., or nearly as long as the lemma. Thus, the L:P ratio (2.0–3.2 in *S. californica,* 1.2–1.7 in *S. Lettermani*) proves to be an excellent character for differentiating these two species, and has valuable applications elsewhere in the genus.

The following key summarizes the characters discussed above which serve to differentiate these two species of *Stipa.*

Leaves filiform, strongly involute; apical hairs of lemma 1.3–1.7 mm. long, 10–19μ thick; awns glabrous or essentially so; L:P ratio 1.2–1.7 ..... *S. Lettermani*
Leaves broader, nearly plane, often becoming involute in dried specimens; apical hairs of lemma 1.5–2.2 mm. long, 20–30μ thick; awns conspicuously pubescent (plumose); L:P ratio 2.0–3.2 ..... *S. californica*

A re-examination of a series of specimens from the Intermountain Herbarium of the Utah State Agricultural College, Pomona College, the United States National Herbarium, and the University of California Herbarium indicates that only a single collection of *Stipa* in California is properly referable to *Stipa Lettermani.* This was collected in Bear Valley, San Bernardino County *(H. S. Yates 6617,* UC). All other reports of the species in the state, including collections from Alpine, Butte, Humboldt, Mariposa, Modoc, Mono, Shasta, Tulare, and Tuolumne counties, are based upon misidentifications.

Stebbins and Love (1944), in their cytological study of Californian forage grasses, have mentioned a chromosome count of *S. Lettermani,* based upon a collection made in Little Last Chance Valley, Plumas County (*Stebbins 2920*). On the basis of the present evidence, this collection is not *S. Lettermani,* and still more interesting, because of its chromosome number, which is 2n=68, it is not referable to *S. californica* either. Since the chromosome number of *S. Lettermani* is 2n=32 (Stebbins, unpubl.), the collection from Plumas County apparently represents an undescribed polyploid related to *S. californica, S. Lettermani,* and *S. occidentalis.*

III. Epidermal Characters in the Californian Species of Stipa

The epidermal cells of the Gramineae were first given serious study by Grob (1896–1897), who called attention to the significance which their characteristics might offer for taxonomic purposes. It was Prat (1932), however, who thoroughly investigated the epidermis and emphasized its features for the characterization of genera and larger groups. Thus, on the basis of epidermal characters, the Gramineae were divided into two main categories, the panicoid and the festucoid. The fact that these two major categories could be progressively subdivided into smaller and

smaller groups by employing the same kind of criteria, has led some authors to consider the nature of the leaf epidermis as important in determining phylogenetic relationships. The Russian cytologist Avdulov (1931), basing his work upon karyological data, developed a new scheme of arrangement for the tribes of grasses, and supplemented his system with the evidence derived from epidermal cells as previously reported by Grob. More recently, Covas (1949) has successfully utilized the epidermis in his study of *Hordeum,* and so did de Wet (1952) in his investigation on *Danthonia* and related genera. As proved to be the case with the L:P ratio, epidermal features have shown their usefulness taxonomically when applied to the Californian species of *Stipa.*

Material and Method. Only herbarium material was used in studying the epidermal cells of the Californian species of *Stipa.* Two slides were prepared for each species and variety, utilizing whenever possible collections as remote from each other geographically as feasible. All observations were made on the abaxial (lower) epidermis obtained from leaves produced at the second internode. The leaves were softened by being placed in boiling water for about ten minutes, and were then transferred to the stage of a dissecting microscope and placed with the axial (upper) epidermis uppermost. The upper epidermis and mesophyll tissues were then gently scraped away with a sharp scalpel, leaving only the lower epidermis. The lower epidermis was cut into small pieces, mounted with the lower surface uppermost on a slide in lactophenol, and covered with a cover glass.

Types of Epidermal Cells. *Stipa* is, according to Avdulov (1931) and Prat (1932), to be included in the Phragmitiformis group of grasses, which is a mixed assemblage of various affinities. The epidermis, in members of this group, however, is festucoid, being characterized by the possession of simple, rounded or elongate, siliceous cells; the minute hairs, if present, are never two-celled. The epidermal cells with important differential characters in *Stipa* may be classified as below.

a. **Long cells.** These are several times as long as broad, are the most numerous element, and comprise the bulk of the epidermis. They show characters of taxonomic value in the variation both in thickness and in degree of undulation of the cell walls, permitting the distinction of three categories of each of these characters.

The walls may be of great thickness as in *S. comata* (fig. 2), of moderate thickness as in *S. Lettermani* (fig. 3), or of slight thickness as in *S. californica* (fig. 4). As to degree of undulation, the walls may be grossly undulate as in *S. comata* (fig. 2), moderately undulate as in *S. californica* (fig. 4), or only slightly undulate as in *S. diegoensis* (fig. 5).

b. **Barb or point cells.** These cells are characterized by terminating in a hair-like upward prolongation (readily visible under the high power objective). They occur either over or between the veins, although both dis-

tributions may occur in the same epidermis, as in *S. californica* (fig. 4). In addition, the intervenous point cells may have either a sharp or a blunt prolongation.

c. **Siliceous cells.** These characteristic cells, distinguished by their high silica content, are divisible into three more or less distinct groups:

Type 1, couple cells. These are composed of two unequal cells, a siliceous cell combined with a suberous one, the smaller showing refringent points which indicate regions in which no silica was deposited (Prat 1932). The couple cells may occur between the veins only, as in *S. californica* (fig. 4), or both between and over the veins, as in *S. comata* (fig. 2).

Type 2, dumbbell or cross-shaped cells. These cells, which Prat (1932) considers as panicoid, are arranged with their long axes parallel to the leaf axis, over the veins. They occur in all species studied except *S. Stillmanii.*

Type 3. These cells are more elongate than the last, have three or more constrictions, and occur only over the veins. They have been found in seven of the nineteen species studied. *Stipa Lettermani* exhibits this type of cell (fig. 3).

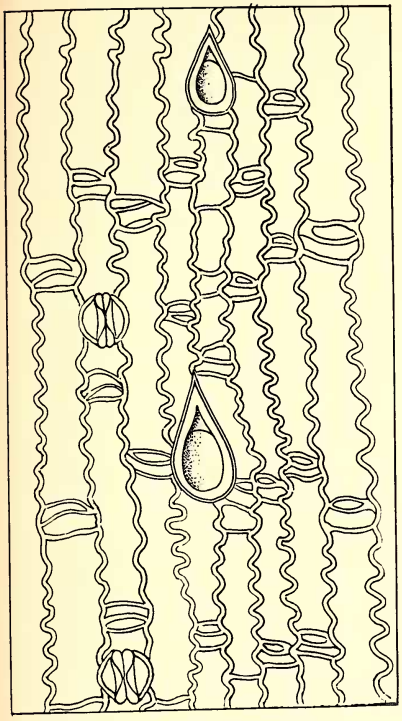
d. **Isolated suberized cells.** These cells are distinguishable by their square shape and darker color, staining red with Sudan IV. They have been found in thirteen of the nineteen species investigated. *Stipa diegoensis* exhibits this type of cell (fig. 5).

e. **Stomata.** Although it is recognized that the stomata may vary in size and shape, only their presence or absence in the abaxial epidermis and their arrangement were taken into consideration in the present study. For the sake of simplicity, the species studied were divided into three groups on stomatal features, as follows: stomata absent, as in *S. Lettermani* (fig. 3); one stomatal row present in some intervenous areas, as in *S. lepida;* two or more stomatal rows present in some or all intervenous areas, as in *S. californica* (fig. 4).

Table 3 presents a general picture of the various types of epidermal cells found in the Californian species and varieties of *Stipa.* As may be seen, these structures readily permit the differentiation of the individual taxa from each other in most instances. Because of the difficulty of observing such anatomical or cytological features, their inclusion in a key for identification appears to be scarcely practicable, although they are useful for more detailed analysis. The following example of *S. Lettermani*

Explanation of Figures 2–5.

Figs. 2–5. Types of epidermal cells. Fig. 2. *Stipa comata,* showing great thickness and gross undulation of the long cell walls; couple cells both between and over the veins, ×950 (*Kennedy 81*). Fig. 3. *Stipa Lettermani,* showing moderate thickness of the long cell walls; siliceous cells Type 2 and Type 3 in black, ×950 (*Yates 6617*). Fig. 4. *Stipa californica,* showing slight thickness and moderate undulation of the long walls, point cells both between and over the veins, siliceous cells Type 2 in black, and two rows of stomatal cells, ×950 (*Stebbins 2942*). Fig. 5. *Stipa diegoensis,* showing slight undulation of the long cell walls, and suberized cells, ×950 (*Gander 5778*).



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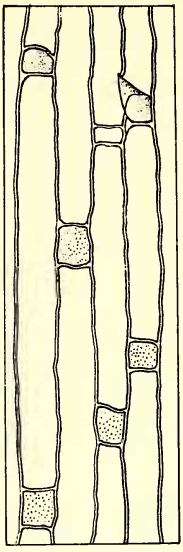

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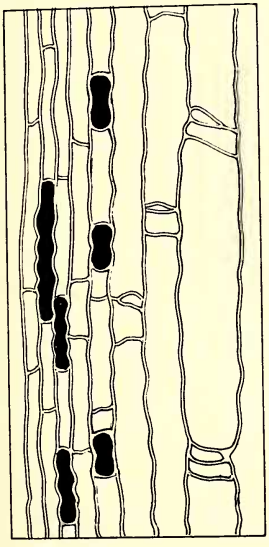

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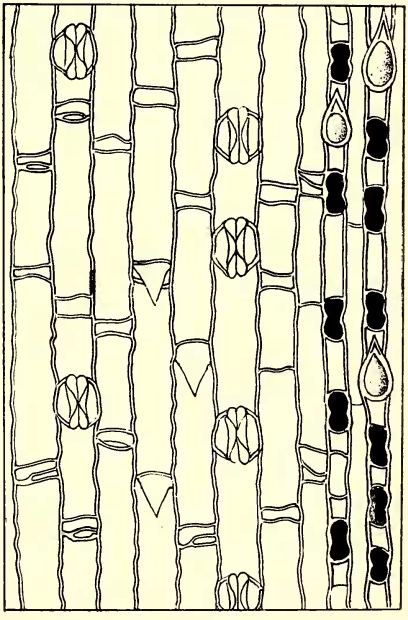

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FIGS. 2–5. Types of epidermal cells in *Stipa*.

Species	Long Cells: Wall Thickness G	Long Cells: Wall Thickness M	Long Cells: Wall Thickness S	Long Cells: Wall Undulation G	Long Cells: Wall Undulation M	Long Cells: Wall Undulation S	Barb or Point Cells: Over the Veins Abs.	Barb or Point Cells: Over the Veins Pres.	Barb or Point Cells: Between the Veins Abs.	Barb or Point Cells: Between the Veins Blunt	Barb or Point Cells: Between the Veins Sharp	Siliceous Cells: Type I —couples— Below veins	Siliceous Cells: Type I —couples— Below + over veins	Siliceous Cells: Type II Abs.	Siliceous Cells: Type II Pres.	Siliceous Cells: Type III Abs.	Siliceous Cells: Type III Pres.	Isolated Suberized Cells Abs.	Isolated Suberized Cells Pres.	Stomata: Abs.	Stomata: 1 row in some intervenous areas	Stomata: 2 or more rows in some or all intervenous areas
S. pinetorum	x			x				x			x	x			x	x		x		x		
S. Thurberiana		x			x			x			x	x			x	x			x	x		
S. Lemmoni		x			x			x	x				x		x	x		x		x		
S. lepida		x			x			x			x		x		x	x			x		x	
S. lepida Andersoni		x			x			x			x	x			x	x			x		x	
S. occidentalis		x			x			x	x			x			x		x	x		x		
S. californica			x		x			x			x	x			x	x			x			x
S. Elmeri			x		x			x			x	x			x	x			x		x	
S. columbiana		x			x			x	x			x			x		x	x		x		
S. columbiana Nelsoni		x			x		x		x			x			x	x						x
S. Williamsii			x		x			x	x				x		x		x	x		x		
S. ordia	x					x		x	x			x			x	x			x	x		
S. diegoensis			x			x		x			x	x			x		x		x			x
S. longiglumis		x				x		x	x				x		x				x	x		
S. Stillmanii	x				x			x			x		x	x		x			x			x
S. coronata	x					x		x	x				x		x	x			x	x		
S. coronata depauperata	x				x		x		x				x		x	x		x				
S. comata	x			x				x			x		x		x	x			x			x
S. comata intermedia		x				x		x	x			x			x		x	x				x
S. speciosa	x			x				x			x		x		x	x			x	x		
S. pulchra		x				x		x			x		x		x	x			x			x
S. Lettermani		x			x			x	x			x			x		x		x	x		
S. cernua		x			x			x			x				x	x			x			x

TABLE 3. OCCURRENCE AND ARRANGEMENT OF EPIDERMAL CELLS IN CALIFORNIA SPECIES OF STIPA.

and *S. californica* shows clearly, however, how entities commonly confused on the basis of grosser morphological characters may be readily separated on features of the epidermis. Thus, *S. californica* has the long cells thin-walled, the intervenous point cells with a sharp prolongation, intervenous siliceous cells of Type 1 (couple cells), and two stomatal rows in some intervenous areas. *Stipa Lettermani,* on the other hand, has long

cells with walls of intermediate thickness, and completely lacks intervenous point cells and stomata on the abaxial epidermis.

The study of the data shown in Table 3 offers a number of other interesting points. Thus, each species has a distinctive combination of epidermal characters. The closest resemblance was shown by *S. californica* and *S. Elmeri*, which are known to be closely similar in their gross morphology and habit. On the basis of epidermal cells, these two species differ only in the distribution and arrangement of the stomata. This fact, however, cannot be generalized, for *S. occidentalis* and *S. Elmeri*, which are also very similar morphologically, have very different combinations of epidermal characters.

On the other hand, *S. lepida* and *S. Thurberiana* are quite different as to gross morphology and habit, but in respect to epidermal characters are very similar, being distinguished only by the arrangement of the stomata.

In summary it can be said that although the epidermal characters have some taxonomic significance the evidence they present for relationship among species may very often be at variance with evidence provided by gross morphology in respect to affinities in the same group of species.

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